

"The Development of *Echinus esculentus*." By E. W. MACBRIDE, M.A., D.Sc., Professor of Zoology in McGill University, Montreal. Communicated by ADAM SEDGWICK, F.R.S. Received November 20,—Read November 28, 1901.

The present communication is to be regarded as a brief preliminary account of an investigation which has occupied my attention for the last three years. The object of this investigation was to examine by means of modern methods the manner in which the various organs of the adult *Echinus* are fashioned out of the corresponding structures of the *Pluteus* larva, and this object has been at last successfully accomplished, and the most important results are briefly described in the present paper.

It was necessary in the first instance to rear the larvæ through the later stages of development in considerable quantities, and the means by which this was accomplished have already been described in two short communications.*

The complete development from fecundation until the conclusion of metamorphosis occupies about 45 days, a period which closely agrees with that required for the development of *Echinocyamus pusillus* as determined by Théel.†

The fertilised eggs become at the end of 24 hours free-swimming ciliated blastulæ; at the end of 48 hours, by the invagination of one side, they are transformed into gastrulæ. The larvæ now assume a somewhat prismatic form, one side becoming flattened and even concave, whilst the opposite one becomes developed into a more or less rounded hump. On the flattened side, about 3 days after fertilisation, the stomodæum makes its appearance as a wide, shallow invagination. The gut has already been differentiated into the three portions, viz., œsophagus, stomach, and intestine, and from the blind apex of the first of these, which has not as yet met the stomodæum, the coelomic rudiment is given off in the form of a flattened sac. This sac rapidly becomes bilobed and then divided into two, the right and left coelomic vesicles.

The longitudinal ciliated band, which is the organ of locomotion, makes its appearance at this time as a thickening round the edge of the concave side of the larva, and at the same time the adoral band appears. This latter, which has the form of a V-shaped loop, projecting

* "Studies in the Development of Echinoidea.—I. The Larvæ of *Echinus esculentus* and *Echinus miliaris*," 'Quart. Journ. Micro. Sci.,' vol. 42, 1899; "The Rearing of Echinoderm Larvæ," 'Journ. Mar. Biol. Assoc.,' vol. 6, No. 1, 1900.

† "The Development of *Echinocyamus pusillus*," 'Trans. Roy. Soc. of Upsala,' 1892.

into the œsophagus, can first be discerned at the age of 4 days after the alimentary canal is completed by the opening of the stomodæum into the œsophagus. It is formed both from the lining of the stomodæum, which is of course ectoderm, and from the endoderm of the œsophagus. This is important, in view of the circumstance that it has been compared to the V-shaped endostyle of the larva of *Amphioxus* (see fig. 1).

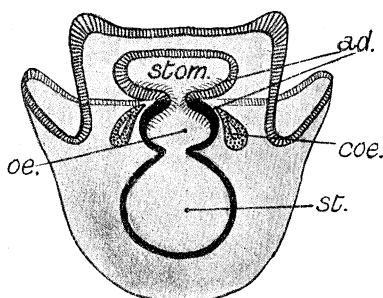


FIG. 1.—Diagrammatic View of a Larva about 4 days old, seen from in front.

ad., adoral band of cilia ; *coe.*, cœlomic vesicle ; *œ.*, œsophagus ; *st.*, stomach ; *stom.*, stomodæum.

By this time, through the formation of outgrowths from the longitudinal ciliated band, the first four arms of the Pluteus have been formed. Even at this early period the left cœlomic vesicle is wider and more thin-walled than the right, and at $4\frac{1}{2}$ days a vertical tubular outgrowth is formed from it, which reaches and fuses with the ectoderm, and in this way the primary pore-canal and madreporic pore are established. These are distinctly structures belonging to the left side. No trace of corresponding structures on the right side was ever observed.

The cœlomic vesicles grow backwards along the sides of the stomach ; that on the left side shows an anterior dilatation into which the pore-canal opens, followed by a constriction and a posterior dilatation. When the larva has reached the age of 8 or 9 days, this posterior dilatation divides into two (fig. 2), the front part being the rudiment of the hydrocœle, whilst the hind part will form the left posterior cœlom, out of which a large portion of the adult body-cavity is formed. The anterior dilatation is the so-called "ampulla" of the stone-canal, and the neck connecting it with the hydrocœle is the stone-canal itself (fig. 3).

About this time the rudiments of the 5th and 6th Pluteus arms make their appearance, and shortly afterwards the right cœlomic vesicle is divided into an anterior and a posterior part. This occurs when the

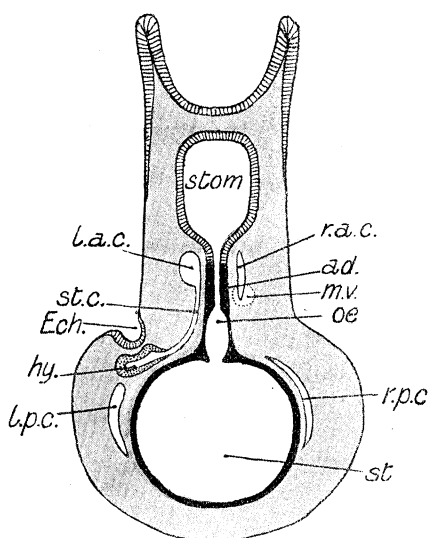


FIG. 2.—Diagrammatic Longitudinal Frontal Section of a Larva about 18 days old.

ad., *æ.*, *st.*, *stom.*, as before; *Ech.*, invaginated ectoderm about to form the oral disc of the future Echinus; *hy.*, hydrocoele; *l.a.c.*, left anterior coelom (ampulla of stone-canal); *l.p.c.*, left posterior coelom; *m.v.*, madreporic vesicle (right hydrocoele—this is not in the plane of the figure); *r.a.c.*, right anterior coelom; *r.p.c.*, right posterior coelom.

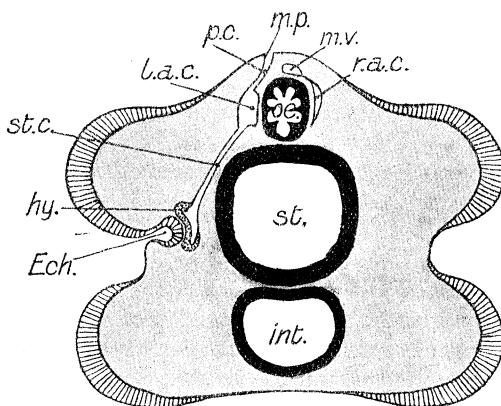


FIG. 3.—Diagrammatic Transverse Section of a Larva about 18 days old.

Names as before; in addition, *int.*, intestine; *m.p.*, primary madreporic pore; *p.c.*, pore canal.

larva is 11 days old, so that by that time the coelom of the larva has completed its transverse segmentation (fig. 4, *d*).

About 13 days a hollow pouch-like invagination of the ectoderm takes place in the region where the hydrocoele is situated, and this is the first trace of the ectoderm of the oral disc of the *Echinus* (fig. 2). At the same time four horizontally placed festoons of the longitudinal ciliated band become separated from the rest and form the "ciliated epaulettes," which are the main organs of locomotion of the larva in the later stages of its development (see fig. 3).

At 16—17 days an outgrowth takes place from the hinder end of the right anterior coelom. It is directed dorsally, and its free end thickens into a nodule of cells which for a brief period is connected with the rest with a string of cells which soon breaks. The nodule then becomes hollowed out, and forms a perfectly closed vesicle lying beside the "ampulla" of the stone-canal. It is the rudiment of the "madreporic vesicle" or "espace sous-madréporique" of the adult, and represents, as I have shown in the case of *Asterina gibbosa*, a rudimentary fellow of the hydrocoele. We may interpret the transient cord of cells as a right stone-canal (see figs. 2 and 3).

Reviewing the development thus far described, it appears that the coelom of the right side of the larva undergoes similar changes to those experienced by the coelom of the left side, but they are slower in their development and this agrees with the facts observed in the case of *Asterina gibbosa*.

The important fact that the coelom of the *Pluteus* underwent transverse segmentation was first made known by Bury* in 1889. His observations were, however, confined to specimens picked out of collections of Plankton, and the series of developmental stages which he obtained was not without considerable gaps. On this account the

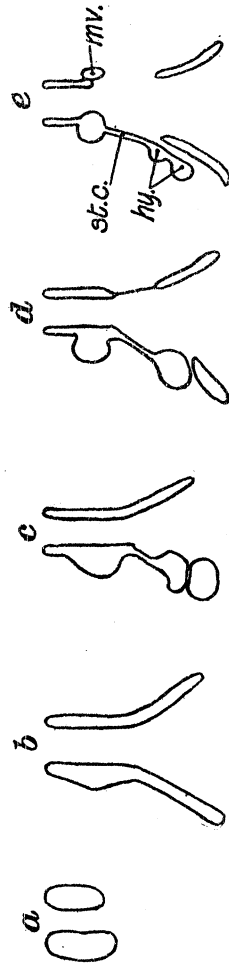


FIG. 4. — Five Diagrams showing the Changes undergone by the Coelomic Vesicles of the *Pluteus* Larva. Names as before.

* "Studies in the Embryology of Echinoderms," 'Quart. Jour. Micro. Sci.,' vol. 29, 1889.

correctness of his views has been often questioned even by Théel.* It affords me much pleasure to be able to completely confirm Bury's views; every stage of the process of the transverse division of the coelom has been observed by me.

At 19—20 days the ectodermic invagination on the left side of the larva has become flask-shaped, and its floor is now in close contact with the hydrocoele. The latter has now taken on the form of a flattened pentagon (fig. 6). It never has the form of an open hoop, so characteristic of the corresponding organ in Asteroidea, Ophiuroidea, and Holothuroidea.

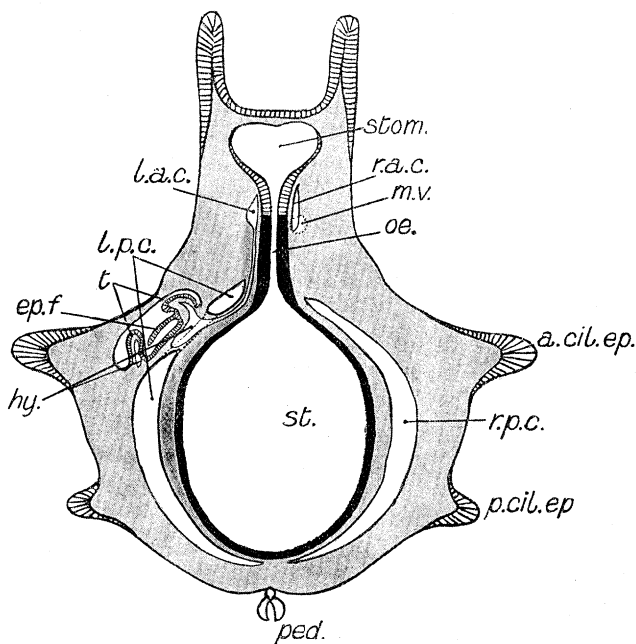


FIG. 5.—Diagrammatic Longitudinal Section of a Larva about 23 days old.

Names as before. In addition, *a.cil.ep.*, anterior ciliated epaulette; *p.cil.ep.*, posterior ciliated epaulette; *ep.f.*, epineural fold; *ped.*, apical pedicellaria; *t.*, primary tube-feet of the Echinus.

About 21 days the rudiments of the last Pluteus arms (the 7th and 8th) appear, and the pentagonal hydrocoele sends out at its corners five projections which are covered by corresponding elevations of the ectoderm. These are the rudiments of the radial canals of the adult, and their terminations form the five primary azygous tube-feet of the young Echinus which correspond to the ocular tentacles of an Asterid.

* *Loc. cit.*

At the same time the ectodermic invagination becomes completely closed: its floor consists of a thick layer of cells which is moulded over the outgrowths of the developing hydrocœle, but its walls and roof remain very thin. Its cavity will be called the amniotic cavity.

The further development of the *Pluteus* consists chiefly in the enlargement of the hydrocœle and of its outgrowths, and of course of the ectoderm covering the latter, and of the amniotic cavity into which they project.

At about 23 days five interradial ridges of the ectoderm, which covers the hydrocœle, make their appearance, alternating with the five primary tentacles. The sides of these ridges grow out into over-arching lamellæ, which soon meet one another, and in this way five epineural canals are formed, opening into a central epineural space (see figs. 5 and 6).

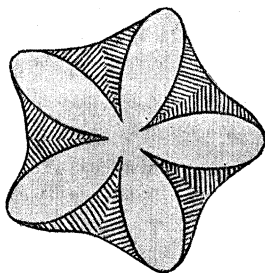


FIG. 6.—Plan of the Hydrocœle (Rudiment of the Water-vascular System) of a Larva about 24 days old.

The wedges (distinguished by cross-hatching) are the epineural folds, which eventually meet one another laterally and form a complete covering over the hydrocœle.

At 26 or 27 days the left posterior cœlom has extended to the posterior apex of the hump, and has there met the right posterior cœlom, forming a thin vertical mesentery. Just above this mesentery the rudiment of the first pedicellaria appears as a little elevation filled with amœbocytes (fig. 5). A little later the rudiments of two other pedicellariæ appear on the right side—one situated dorsally, the other ventrally.

The left posterior cœlom, which was at first situated entirely posterior to the hydrocœle, has by this time grown completely round it in a circle, and in the axis of this circle the stone-canal still connects the "ampulla" or anterior cœlom and the hydrocœle (fig. 5).

At 27—28 days the rudiments of the masticatory system of the so-called "Aristotle's lantern" make their appearance. These are five outgrowths of the left posterior cœlom, having the shape of inverted

wedges, which alternate with the five radial canals which have been developed from the hydrocœle (fig. 7). These outgrowths soon lose

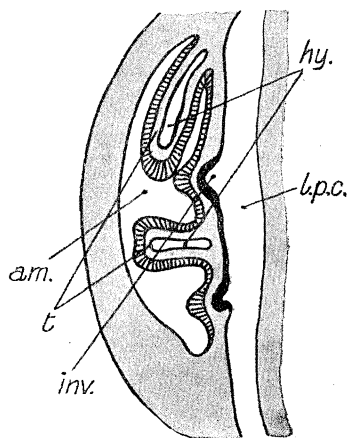


FIG. 7.—Diagrammatic Section of the developing Oral Disc of the future Echinus in a Larva 26 days old.

Names as before. In addition, *am.*, amniotic cavity; *inv.*, invaginations of coelomic epithelium, which are the rudiments of the perihæmal spaces and of the “lantern coelom.”

their connection with the coelom, and become converted into closed sacs. From each of them a narrow outgrowth sprouts out, which insinuates itself between the water-tube and the ectoderm of the base of the tentacle. In this way the radial perihæmal canals are formed. The main body of the sac, however, forms a tooth-sac (fig. 8). From its floor an upstanding projection is formed, which is the root of the tooth, whilst from its sides the alveoli, which constitute the jaw, are formed. Calcification, however, proceeds in these parts only to a very slight extent till after the metamorphosis.

By the time the larva has attained an age of 32—33 days, the primary tube-feet have become long, and have acquired their suckers, and, in addition, a curious little sensory prominence, consisting of elongated ectoderm cells situated in the centre of the sucker; the three pedicellariæ mentioned above are fully developed, and the four primary ciliated epaulettes have grown so as to almost meet one another, and thus form a complete circle. In addition, two secondary ciliated epaulettes have been formed in a more posterior position (see fig. 5); these extra epaulettes are characteristic of *Echinus esculentus* as opposed to *Echinus miliaris*.

The larva continues to grow up to 36—38 days after fecundation. By that time several important changes have taken place. The hydro-

cœle and amniotic cavity have grown so as to occupy the entire side of the larva; the tube-feet are long, and show wriggling movements. Spines have commenced to make their appearance; one or two small quadrangular rudiments are situated at the sides of the posterior pedicellaria, but, in addition, there are ten conical outgrowths of the oral disc of the *Echinus*, *i.e.*, of the floor of the amniotic cavity, alternating with the radial canals.

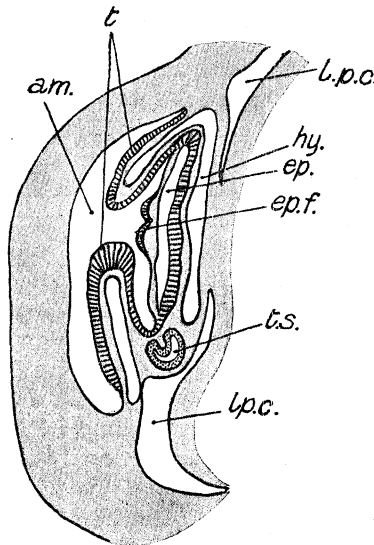


FIG. 8.—Diagrammatic Section of the developing Oral Disc of the future *Echinus* in a Larva 30 days old.

Names as before. In addition, *ep.*, epineural space; *ep.f.*, epineural fold; *t.s.*, tooth-sac (developed from the invagination of cœlomic epithelium shown in fig. 7).

The first trace of the adult mouth and œsophagus appears as an invagination of the oral disc, indenting the centre of the hydrocœle. At a later period it completely perforates the hydrocœle, thus converting it from a flattened plate into a ring. The adult œsophagus is thus shown to be a stomodæum. The stomach loses its globular form, and becomes flattened on the side towards the hydrocœle.

About this time the first trace of the so-called "blood-system" becomes apparent. From the beginning the wall of the gut has at no time been in actual contact with the cœlomic wall. Always there has intervened a layer of jelly with a few amœbocytes in it, the same substance which exists in much greater quantity between the outer wall of the cœlom and the ectoderm.

At about 36 days the jelly intervening between the cœlom and the

gut becomes profoundly altered in chemical composition. It acquires staining properties, but the amœbocytes contained in it remain glassy and clear. At the same time, the gut-cells become more difficult to stain, pointing clearly to the exudation of proteid matter from the gut-cells into the surrounding jelly. From this envelope of altered jelly the mesenteric and anti-mesenteric vessels of the adult are developed.

The metamorphosis commences at about 40—42 days. By that time the amniotic cavity, the hydrocœle, and the underlying left posterior cœlom have grown so greatly that the posterior epaulettes and the pedicellaria in the centre of the aboral surface are pushed to one side. In other words, the preponderant growth of the organs of the left side, which in *Asterina gibbosa* becomes evident at an early period of development, here makes its appearance only just before metamorphosis. From the anterior end of the left posterior cœlom a cellular rod grows out, burrowing into the jelly lying between the ampulla and the right hydrocœle. This is the rudiment of the "ovoid gland," or so-called "heart," which here, as in *Asterina gibbosa*, is in reality a genital stolon. The anus closes up, and the mouth closes also about the place where the stomodæum joined the larval œsophagus. The Pluteus arms have become shorter and thicker, and a hole has appeared in the roof of the amniotic cavity through which the tube-feet are protruded.

The larva now sinks to the bottom, and in a very short time the ciliated band and the "epaulettes" disappear, being devoured by amœbocytes. The roof of the amniotic cavity is entirely abolished, and the young *Echinus* creeps about freely on its five tube-feet. The rudiments of a second pair of tube-feet are already present in each radius, but are not yet functional. The arched dorsal surface, with its spines and the three pedicellaria, is at this time greater in extent than the ventral ambulatory surface, so that it may be said that the young *Echinus* passes through an Asterid stage in development.

The whole ambulacral surface, however, grows rapidly in comparison with the dorsal surface; the terminal tube-feet become smaller, and are eventually sunken in grooves in the test. They become adherent to the sides of these grooves, and so the long flexible tube-foot of the just metamorphosed *Echinus* becomes changed into the insignificant ocular nodule of the adult.

Compared with the development of *Asterina gibbosa*, the development of *Echinus esculentus* must be regarded as being very much modified; nevertheless, all the main features of the development of *Asterina* can be recognised in *Echinus*.

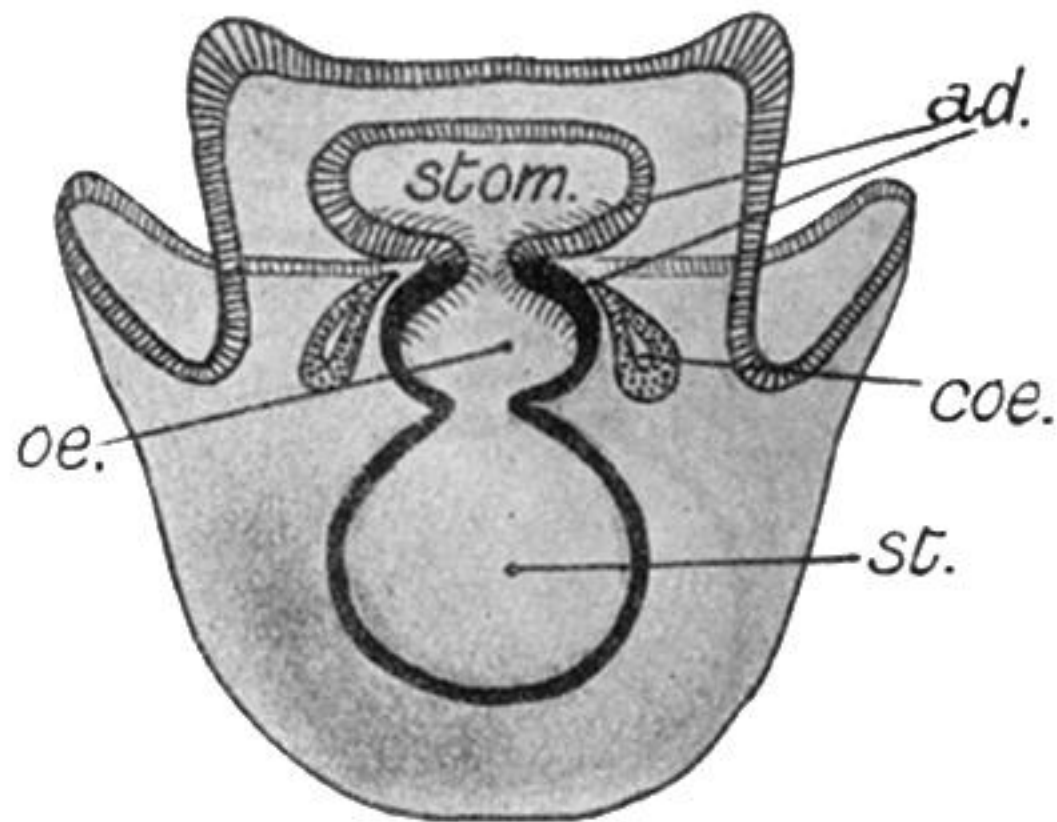


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ad., adoral band of cilia ; *coe.*, coelomic vesicle ; *oe.*, oesophagus ; *st.*, stomach ;
stom., stomodæum.

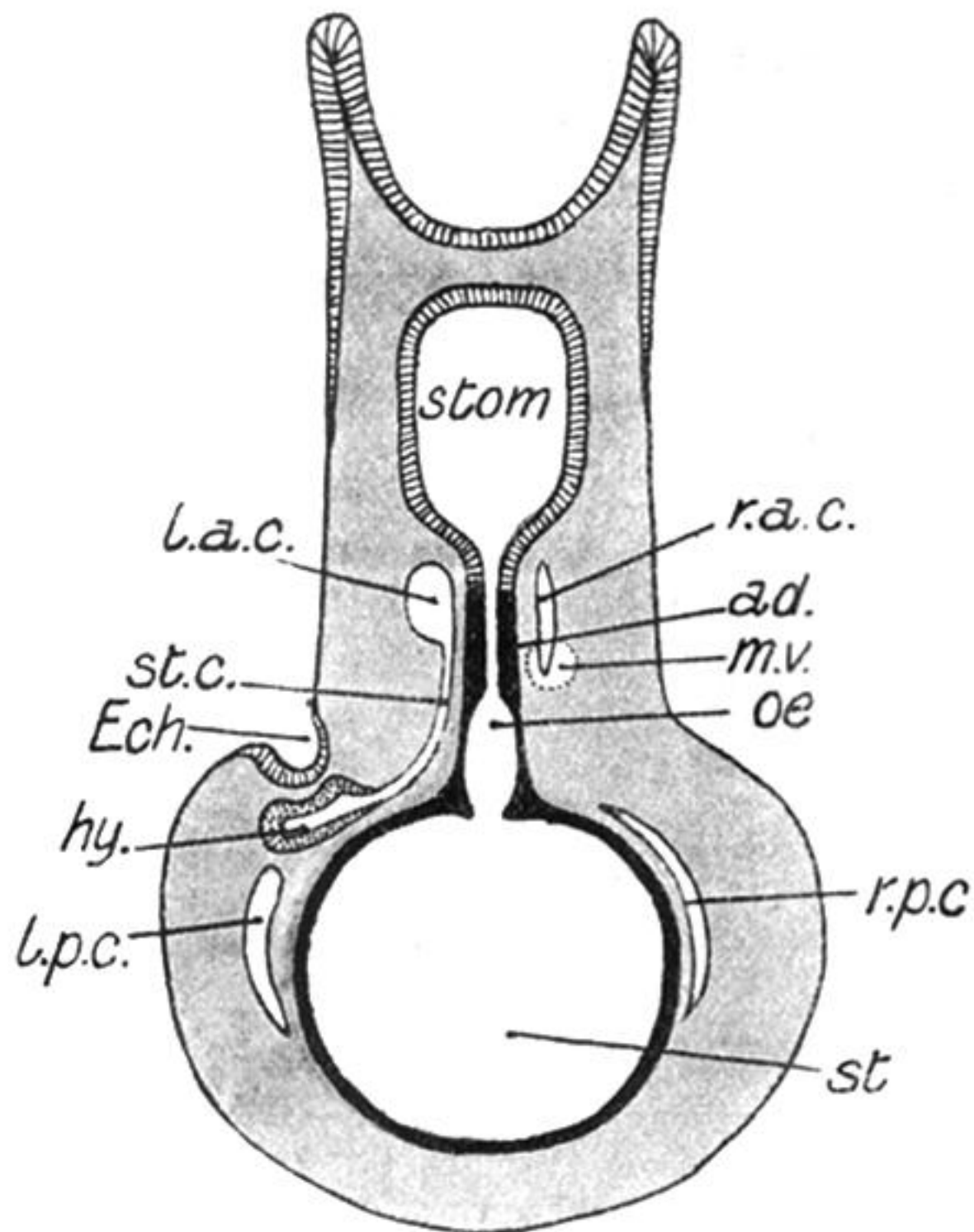


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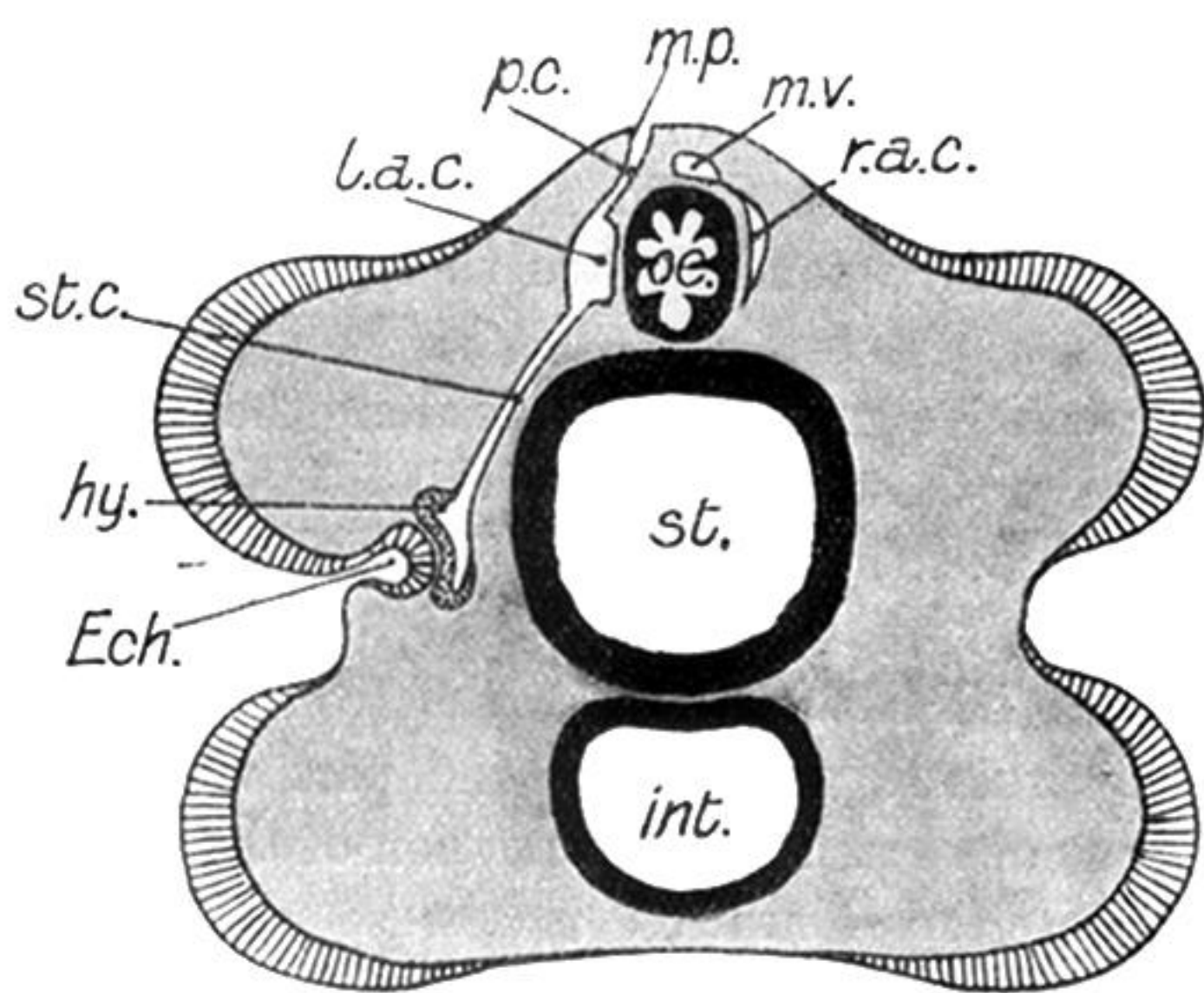


FIG. 3.—Diagrammatic Transverse Section of a Larva about 18 days old.

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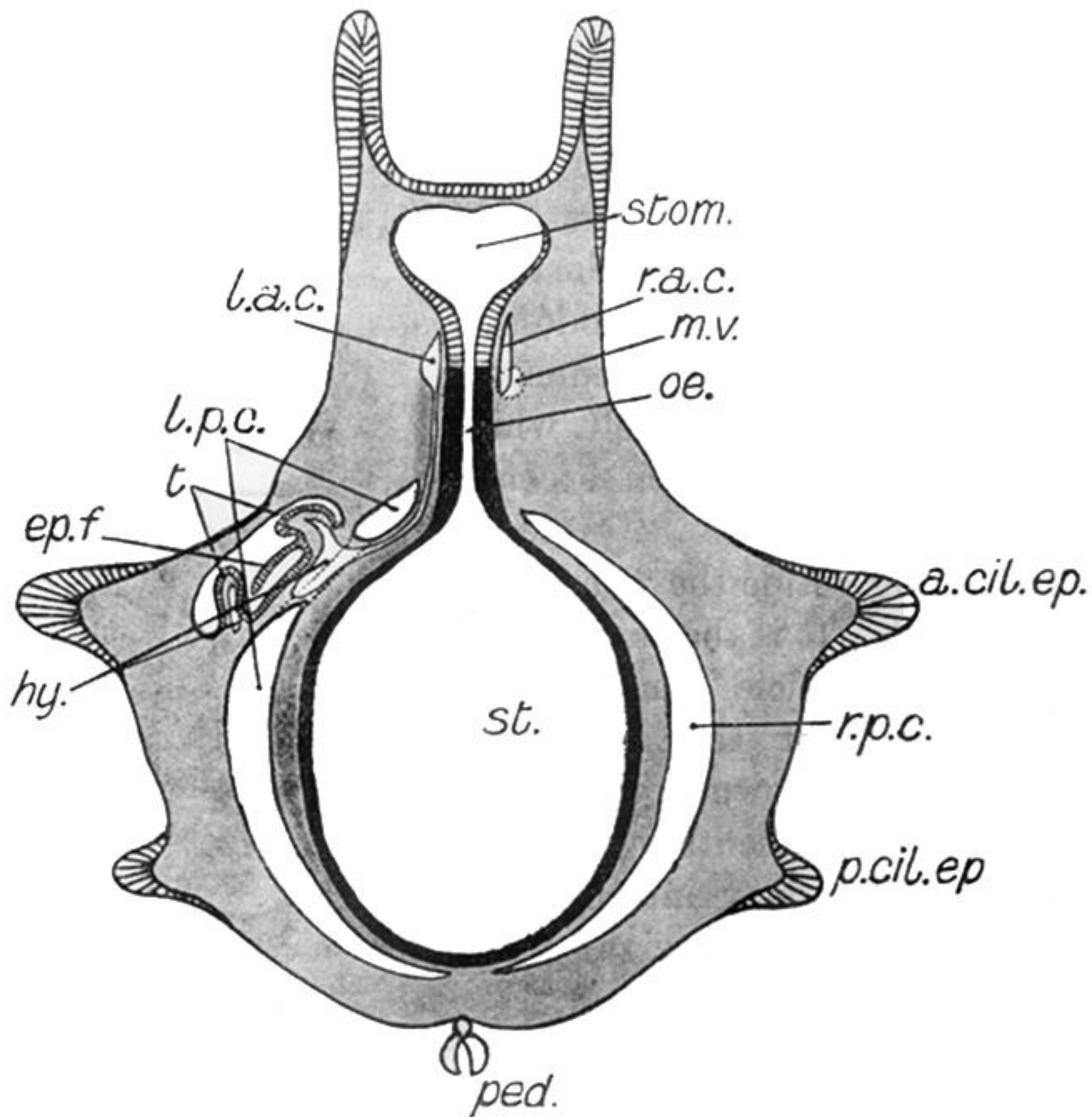


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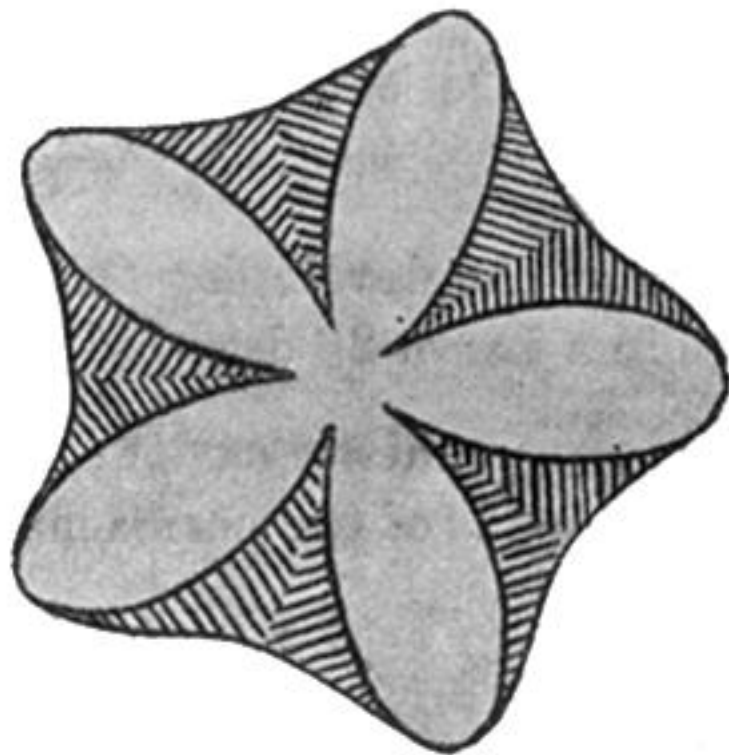


FIG. 6.—Plan of the Hydrocoele (Rudiment of the Water-vascular System) of a Larva about 24 days old.

The wedges (distinguished by cross-hatching) are the epineural folds, which eventually meet one another laterally and form a complete covering over the hydrocoele.

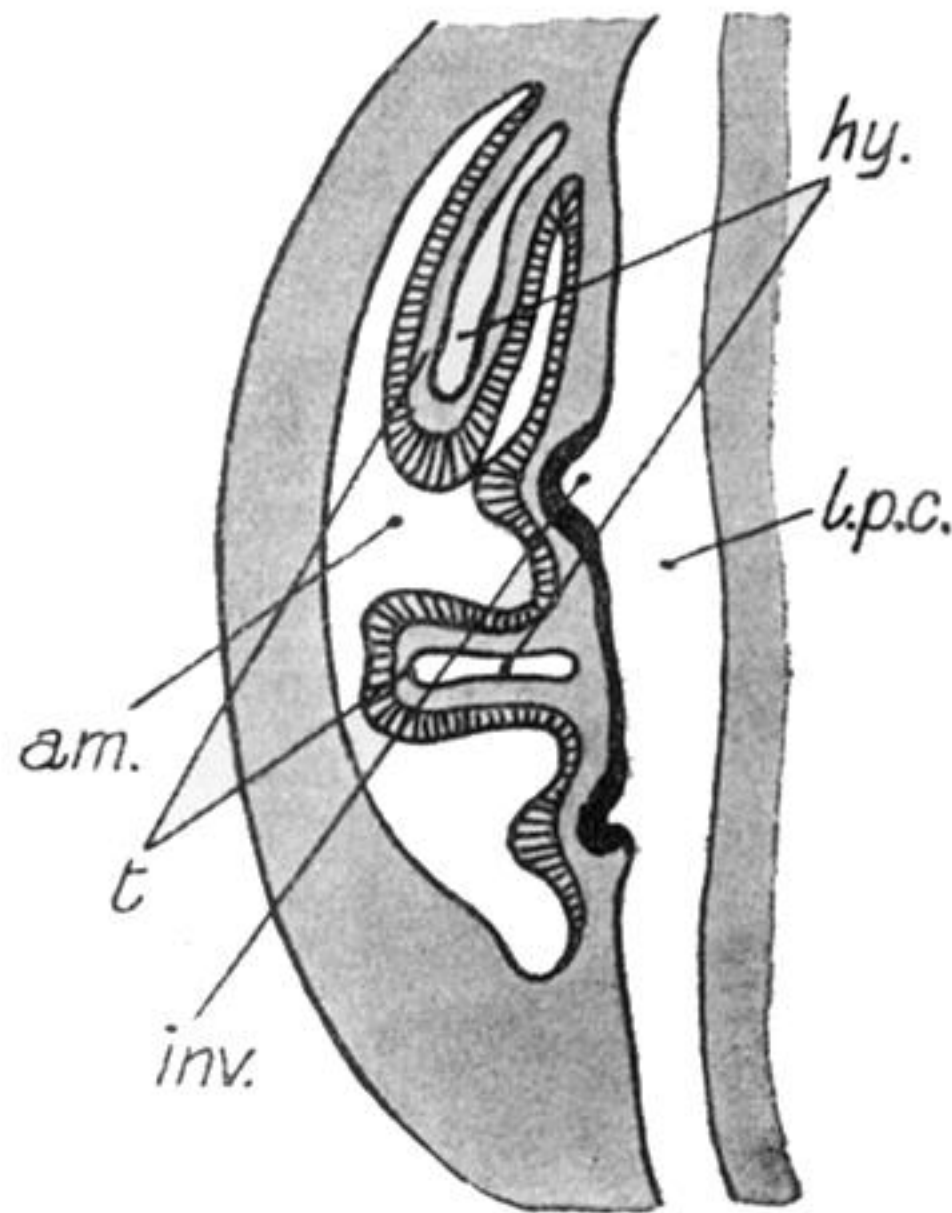


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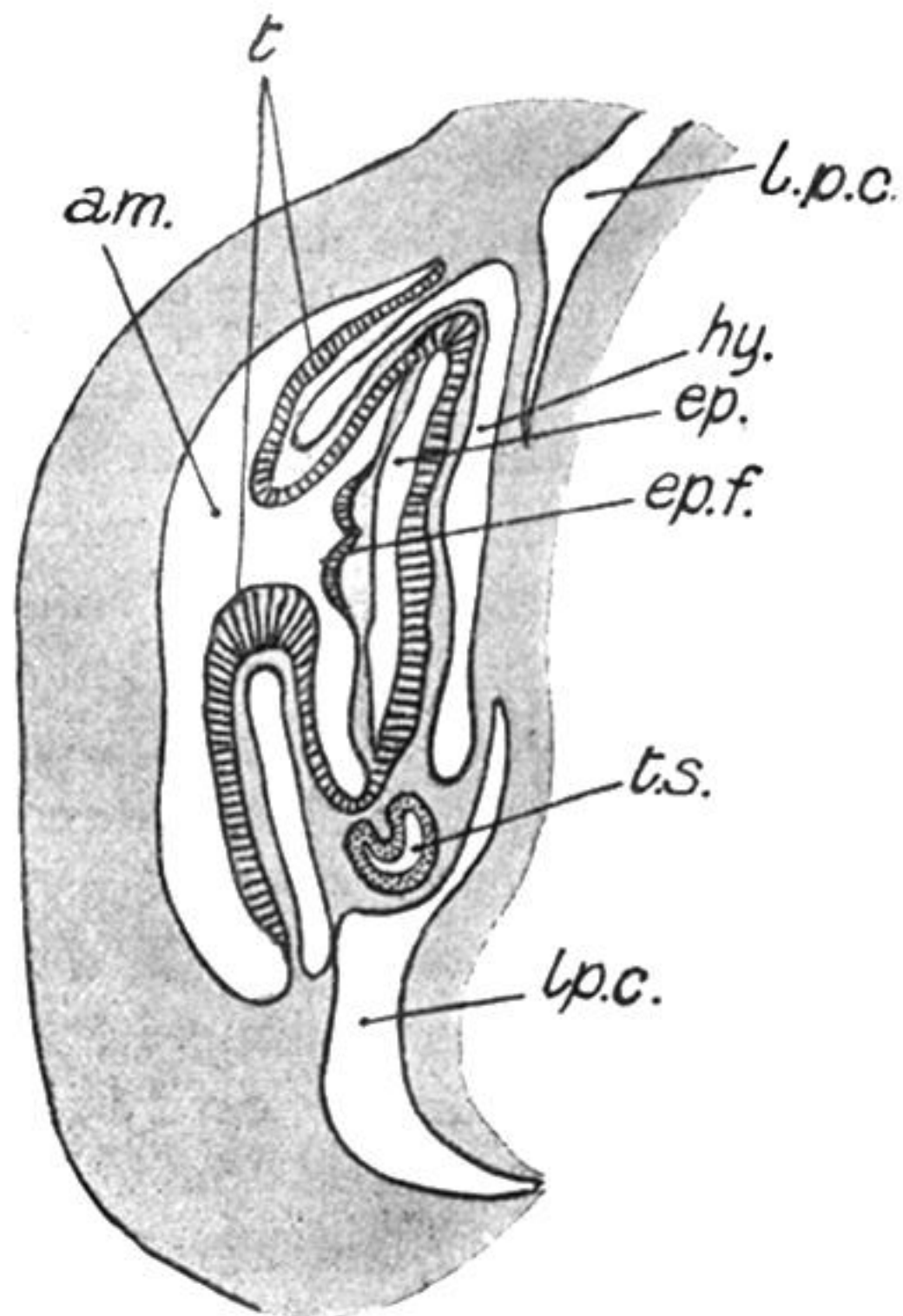


FIG. 8.—Diagrammatic Section of the developing Oral Disc of the future Echinus in a Larva 30 days old.

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